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Leaf-to-aircraft measurements of net CO_2 exchange in a sagebrush steppe ecosystem

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[1] Measurements of net CO_2 flux density (μmol m^{-2} s^{-1}) from a high elevation, sagebrush steppe community in southeastern Wyoming (USA) were compared quantitatively among four different instrument systems (leaf cuvette and 1 m^2 community chamber for gas exchange measurements; tower and aircraft eddy covariance systems) by minimizing spatial and temporal variability. Ground-based flux measurements were recorded at an intensive site located near the midpoint and directly beneath an approximate 20-km flight transect. A high degree of homogeneity in plant species composition, density, cover, and the amount of leaf area per unit ground area, as well as little topographic variability, was measured at the intensive site and along the flight transect. Flux measurements were compared on days with relatively high and low soil moisture availability (predawn plant water potentials >-0.8 MPa and <-2.0 MPa, respectively). Same-day, mean flux values between the four measurement systems (4.0–4.6 μmol m^{-2} s^{-1}) over identical time intervals (0900–1100 hours) varied by a maximum of ±9% (maximum range 23%). Ground-level measurements taken within ±1 day of flight measurements, varied by a minimum of ±7% (25% maximum range) of aircraft values. This difference increased curvilinearly to a maximum of ±31% (38% maximum range) for a 2-week separation between flight and ground-based measurements. Thus, under near-ideal conditions of topographic and vegetative homogeneity, temporal heterogeneity in the measurement regime of only a few days resulted in greater disparity in measured CO_2 flux density than occurred among the four instrument types. *INDEX TERMS:* 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 0322 Atmospheric Composition and Structure: Constituent sources and sinks; 0330 Atmospheric Composition and Structure: Geochemical cycles; *KEYWORDS:* CO2 flux, sagebrush steppe, aircraft, tower, eddy covariance, leaf

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1. Introduction

[2] Accurate measurement of CO_2 exchange between different terrestrial ecosystems and the atmosphere continues to be a high priority due to the accumulating evidence for global warming and the recent affirmation that atmospheric CO_2 is the dominant greenhouse gas [*Shackleton*, 2000]. These measurements will provide, ultimately, a quantitative closure of the Earth's annual and interannual carbon budget, as well as the capability for predicting future impacts of anthropogenic CO_2 on such important processes as biogeochemical cycling [*Canadell et al.*, 2000]. To facilitate this objective, organizations such as AmeriFlux of North America, CarboEurope, and the global FLUXNET program are examples of current efforts to standardize and consolidate measurements of CO_2 flux from the major terrestrial landscapes of the Earth [e.g., *Running et al.*, 1999; *Canadell et al.*, 2000; *Baldocchi et al.*, 2001a]. Currently, the use of eddy covariance towers dominate the global effort to quantify CO_2 exchange dynamics, although this technique has a relatively large footprint size and lacks the capability for more mechanistic studies [*Baldocchi et al.*, 2001b].

[3] Fundamental questions are still unanswered concerning the choice of a particular experimental approach and corresponding instrumentation that might be effective for measuring CO_2 exchange from native and agricultural landscapes. Current measurement systems include leaf- and branch-level cuvettes, larger chambers that can sample entire plants, or even small community segments, as well

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as towers and aircraft that sample much greater spatial areas with sampling footprints encompassing km^2 (see *Canadell et al.* [2000] for a review). For natural landscapes, in particular, large spatial and temporal heterogeneity makes accurate comparisons among different instrument systems challenging [e.g., *Goulden et al.*, 1996; *Ruimy et al.*, 1996; *Oechel et al.*, 1998]. While plant-level measurements provide a more mechanistic and evolutionary "bottom-up" approach, towers and aircraft provide a much more integrative "top-down" approach directly applicable to the ecosystem level. However, both approaches are valuable in that each provides a useful perspective for understanding mass exchange processes [*Canadell et al.*, 2000].

[4] Ultimately, the choice of a particular measurement scale (and appropriate instrument system) involves not only an evaluation of scientific objectives (mechanistic versus integrative resolution) and economic constraints, but also requires foremost an appropriate analysis of accuracy. For example, plant-level measurements are less expensive per sample day and more revealing in terms of species-level mechanisms, but are also labor intensive, requiring large sample sizes for adequate spatial and temporal replication. In contrast, aircraft measurements are much more integrative spatially and, yet, can be extremely expensive per sample day. Thus, the greater spatial coverage of the aircraft approach is often restricted by the large expense necessary for initial start-up and subsequent temporal replication. In particular, the capability for scaling plant-level measurements to the ecosystem level would provide a mechanistic approach, as well as integrative values of net CO_2 exchange. Yet, only a few studies have made comparative evaluations of the methods and instruments currently available for measuring CO_2 flux, and these studies have been clouded by relatively large spatial and temporal sources of heterogeneity in the sampling design [e.g., *Oechel et al.*, 1998]. However, it is encouraging that, despite these sources of error, reasonably comparable values of net ecosystem CO_2 flux have been reported for a gas exchange community chamber, an eddy covariance tower, and an eddy covariance aircraft measurement system deployed in an artic tundra ecosystem [*Oechel et al.*, 1998].

[5] The purpose of the current study was to provide a quantitative comparison of net CO_2 flux measurements that range in scale from the branch and community segment, to the much larger spatial scale of the tower and aircraft. A primary focus was to reduce spatial and temporal sampling variability to the minimum possible so that differences among instrument platforms would be possible utilizing state-of-the-art methodology and instrumentation. Temporal heterogeneity was then evaluated by comparing repetitive measurements with all instrument systems on identical days within the same 2-hour periods, and during representative days with contrasting high and low net CO_2 flux values measured for the growth season. Spatial heterogeneity was also minimized by selecting a homogeneous vegetation type (determined by sampling vegetation composition along the full length of the aircraft transect) over a large area (>400 km^2) with little topographic variation (<140 m elevation change across a northeast-facing aspect with a mean slope of<3% rising to the south) or microtopographic variation (surface features), and by taking all ground-based measurements directly beneath the transect flown by the aircraft. Analysis of temporal effects on measured CO_2 flux was accomplished by grouping measurements according to the number of days that separated measurements between any of the four instrument systems, i.e., same-day measurements for all systems, and when measurements were made within a given number of days of one another. The specific instrument systems employed here, along with their estimated "footprint" size in parentheses, included leaf/branch gas exchange cuvettes (cm^2), a 1-m^{-2} gas-exchange chamber for combined plant and soil fluxes (m^2), plus a tower (dm^2) and aircraft (km^2) that were both equipped with eddy covariance measurement systems. CO_2 flux density was expressed on the same per unit ground basis according to standard techniques for quantifying vegetative cover of dominant species measured at randomly selected sites along the full length of the flight transect, as well as at the intensive measurement site located at the midpoint of the flight transect. In this manner, temporal sources of error due to different sampling times were minimized, along with potential spatial errors due to differences in vegetation. These comparisons might also provide an estimate of the maximum accuracy (least-error) possible for characterizing net CO_2 exchange (net ecosystem exchange) from a natural landscape.

2. Methods and Materials

2.1. General Methodology

[6] During midsummer, net flux densities of CO_2 (μmol m^{-2} s^{-1}) were measured continuously during 2-hour morning periods using leaf/branch cuvettes, a 1-m^{-2} community chamber, and a tower eddy covariance system when the aircraft (eddy covariance) was flying replicate transects directly overhead. Thus, all same-day measurements were made within minutes of one another during mornings under clear skies and relatively high flux values for the summer (June 21 and 22, 2000), as well as on a day (July 7, 2000) with relatively low flux following an extended drought period that generated substantially lower plant water potentials. The aircraft flew a 19-km transect over a homogeneous stand of sagebrush steppe, and directly over the ground-level site at the approximate middle of the flight transect where all other measurements were being taken concurrently (leaf/branch cuvette, 1 m^{-2} chamber, tower). Branch-level measurements of photosynthetic CO_2 exchange from the dominant plant species were taken almost simultaneously with chamber measurements of 1-m^2 plots selected as representative of the landscape (i.e., based on specific values of plant species and exposed ground cover). During replication of both the branch cuvette and 1-m^2 chamber measurements, the eddy covariance tower was monitoring CO_2 exchange continuously at a location within 100 m upwind of the branch cuvette and community chamber measurements, and directly beneath the aircraft flight line. Ground-level measurements of CO_2, including tower values, did not show any significant change within ±10 min of the time the aircraft passed overhead, indicating no effect of aircraft emissions on ground-level CO_2 concentrations.

2.2. Research Site

[7] Sagebrush steppe often dominates low-elevation basins below about 2500 m elevation in the northern Rocky

Mountains and Great Plains of Wyoming, Montana, and North and South Dakota west of the Missouri River, as well as the adjacent highlands of Idaho and Utah. Surface area coverage of this dominant community is estimated to be 22% of the total land area of Wyoming [*Merrill et al.*, 1996]. Percent cover of this type of open sagebrush steppe in all of North America is estimated to be ~16% of the total vegetative land cover, compared to ~26% for total global coverage [*Loveland and Belward*, 1997; *Loveland et al.*, 1999; *DeFries and Los*, 1999].

[8] The intensive study site was located in the Shirley Basin at 42°18′N, 106°34′W and ranges from ~2050 to 2200 m in elevation (2193 m mean elevation). The dominant species of this shrub-steppe community is Wyoming big sagebrush (*Artemisia tridentada* Nutt. ssp. *wyomingensis* Beetle and Young), although the perennial grasses *Poa cusickii* Vasey, *P. sandburgii* Vasey, *Pascopyrum smithii* Rybd., and *Astragalus miser* Dougl. ex Hook. contributed measurable amounts to the total plant cover, especially during the wetter portions of spring and early summer (Table 1). Annual precipitation at this site has averaged 246 mm and mean annual temperature was 4.3°C based on mean values of continuous records for 1951–1980 [*Martner*, 1986]. Between two thirds and three fourths of this annual precipitation can come as snow during winter, especially the wetter snows of spring and fall [*Fisser*, 1984a, 1984b]. Long-term precipitation and temperature data for each site were obtained from the nearby (~9 km) weather station in the Shirley Basin, Wyoming (42°22′N, 106°06′W). Temperature and precipitation data for summer 2000 were also recorded on site using shielded thermocouples and a tipping-bucket rain gauge located at the approximate center of the intensive site. The soils of this area are colluvial soils consisting of fine loamy clays with an abundance of limestone fragments and are classified as Ustic Haplargids and Ustic Natragids [*Love and Christensen*, 1985]. The specific research site was originally chosen as representative of the topography and homogeneity of plant cover in the region, and along the flight line of 19 km, based on existing plant surveys from Landsat Thematic Mapper (TM) images and aircraft photography [*Driese et al.*, 1996]. Subsequent, randomized quadrat sampling quantified the degree of vegetative homogeneity at the intensive site and along the full length of the flight transect.

2.3. Vegetation Sampling

[9] To convert the CO_2 flux density measurements for the branch cuvette and 1 m^2 community chamber to values comparable to tower and aircraft measurements, the amount of total leaf area per unit ground area was quantified for the summer growth periods during the summers of 1998–2000 (21 May to 19 September) over 2-day sampling periods, and within ±11 days of aircraft flight dates. Six randomly selected transects were sampled during 1998, four in 1999, and four during the summers of 2000 and 2001 each, within 2.6 km of both sides of the flight transect line. All of these data were used to test for homogeneity (evenness) of the vegetation [*Pielou*, 1966; *Ghent*, 1991] across the transect length and width, and to convert measured CO_2 exchange to a unit ground area basis for comparison with concurrent 1-m^2 chamber, tower, and aircraft flux measurements. Percent cover (projected area per unit ground are) for each of the dominant species was determined according to the point intercept method described by *Floyd and Anderson* [1982]. A total of six line transects were also established at the intensive site (100–250 m in length) and nearest-neighbor sampling was conducted at 5–10 locations selected randomly along transects. The amount of leaf area per unit ground area (LAI) was also estimated independently by clipping and measuring the total leaf area per unit ground area for 1-m^2 plots selected randomly along each transect (N = 5 on six of the sixteen total transects for a total sample size of 30 plots). Plant crown size (greatest length and width) was compared to leaf area and found to be highly correlated, as previously reported by *Rittenhouse and Sneva* [1977] and *Ganskopp and Miller* [1986]. Thus, replication of crown size measurements for sagebrush was used to estimate leaf area per unit ground area for the dominant shrub *A. tridentata wyomiensis* and associated grass and forb species that were present and exchanging measurable CO_2 during the sampling periods. Leaf area per unit ground area for sagebrush was computed using the best fit regression equation y = 2.44 + 0.786 log(crown diameter) + 0.320(orthogonal diameter) + 1.24 log(maximum crown height) with an r^2 of 0.95 [*Rittenhouse and Sneva*, 1977]. An identical approach was used for converting grass and forb percent cover to leaf area per unit ground area when grass species were photosynthetically active (until the end of June). For the flight, transect percent cover was also estimated from photographs (converted to digital format using a Sony MVC-FD91 digital camera) of the randomly selected quadrats scanned into a computer image analysis program (Scion Image, National Institutes of Health). All values of percent cover were then used to convert photosynthetic CO_2 flux density values measured with the leaf/branch cuvette to flux per unit ground area, allowing direct comparisons between all four measurement systems.

Table 1. Vegetative Characteristics of the Intensive Measurement Site Located at the Midpoint of the Flight Transect and for All Transects Selected Randomly Along the Full Length (~19 km) and Breadth (~4 km) of the Flight Transect Within the Sagebrush-Steppe of the Shirley Basin, Central Wyoming[a]

Plant	Percent Cover	Number/m^2	LA, m^2/m^2
Sagebrush	15.2 ± 5.0	3.6 ± 1.1	0.33 ± 0.7
Grasses	24.3 ± 5.9	19.1 ± 5.2	0.21 ± 0.7
Forbs	10.1 ± 3.3	6.4 ± 1.3	0.06 ± 1.2
Soil	45.4 ± 11.1	–	–

[a]A total of six transects at the intensive site and twelve transects along the full length and breadth of the flight transect were sampled randomly (see text) for each of the three summers between 1998 and 2000. Parameters are percent plant cover (projected area of crown),percent exposed soil, number of plants/m^2, and leaf area (LA) per unit ground area (m^2/m^2). Individual plants of grass species were not distinguished from individual ramets (asexual sprouts and tillers). No statistical differences were found among transects at the intensive site or for any of the 12 individual transects along the flight path (ANOVA, N = 60, $p < 0.05$), or when comparing individual transects selected randomly within the single intensive site (ANOVA, N = 30, $p < 0.05$). Thus, all transect data were pooled for averaging according to plant type (sagebrush, grass, forb). Plus and minus values are 95% confidence intervals.

2.4. Eddy Covariance Aircraft

[10] Airborne CO_2 flux measurements were made using the University of Wyoming King Air research aircraft during repeated, level passes along transects over each site

at altitudes of ~60–90 m above ground level. All aircraft flights were initiated in the middle to late morning (0900–1100 hours) under clear skies with variable, light winds (<16 km/hr) from the northwest, ensuring a representative estimate of summer photosynthesis patterns and allowing measurements to be completed before the onset of widespread convective cloud formation typical of afternoon periods. Estimated footprint size for the aircraft was ~2–3 km with eddies of from 1 to 3 km occurring outside the surface layer. Thus, smaller-scale variation such as riparian drainages and small water impoundments were not discernible. During measurement periods, wind speeds at ground level (2 m height) varied between 1.8 and 2.6 m s^{-1} from the northwest, and a sun-heated surface layer generated sensible heat fluxes of between 99 and 184 W m^{-2} for the July dates (as measured by the tower), and latent heat fluxes of between 135 and 191 W m^{-2}, indicating fully turbulent conditions during the sampling periods [*Dabberdt et al.*, 1993; *Goulden et al.*, 1996]. Identical values for the July 7 date were 99 to 73 W m^2, respectively. CO_2 flux density values are indicated as positive when net CO_2 movement was toward the surface. A total of 12 passes along the transect were made on June 21, four on June 22, and twelve on July 7, with each successive pass being flown in the opposite direction. Each transect pass required about 7–8 min. All values are simple arithmetic means of the multiple flux values measured for up to eight low-level passes along the flight transect on a given sampling day. CO_2 flux values were computed as positive when net CO_2 movement was toward the surface (photosynthetic sink).

[11] The King Air aircraft is a twin-turboprop, Beechcraft KingAir currently operated and maintained within a National Science Foundation Site Facility and administered by the Department of Atmospheric Sciences, University of Wyoming [see *Kelly et al.*, 2002]. The CO_2 measurement system within the aircraft is designed for low-altitude sampling along transects using fast response sensors. It is fully equipped for measurement of 3-D winds, temperature, and water vapor and CO_2 concentrations, allowing resolution of eddy covariance fluxes of momentum, sensible heat (frequencies up to 10 Hz), latent heat, and CO_2 at frequencies up to 2 Hz. Analog signals from the various sensors are first passed through anti-alias, low-pass filters having cutoff frequencies of 10 Hz, and are then digitized at sampling rates of 50 Hz. The 3-D wind vectors are calculated from a combination of measurements by a nose-boom gust probe, a laser-ring inertial navigation system, and a global positioning system (GPS) receiver. The fast-response temperatures are measured with small-diameter thermistors in a Rosemount housing. The water vapor and CO_2 concentrations were measured with a LICOR 6262 infrared absorption spectrometer modified for maximum response times [*Auble and Meyers*, 1992]. A more detailed description of the instrumentation, as well as results of flights comparing tower estimates of eddy fluxes with flight measurements, are given by *Desjardins et al.* [1993] and *Dobosy et al.* [1997]. Updates from that configuration include (1) using reference gas from an onboard cylinder for the LICOR 6262 infrared gas analyzer, rather than recirculating chemically scrubbed air, and (2) a new data system which samples signals at 100 Hz after anti-alias, low-pass filtering with a filter cutoff frequency of 20 Hz. The flight data were archived at 20 Hz after post-flight processing. Carbon dioxide fluxes were calculated from the covariance of air vertical velocity and CO_2 concentration, after first removing linear trends from both time series for each pass.

2.5. Eddy Covariance Tower

[12] Measurements of carbon dioxide, sensible heat, and water vapor exchange were taken continuously using standard eddy covariance methods and assumptions [*Leuning et al.*, 1995; *Baldocchi et al.*, 1986; *Miranda et al.*, 1997; *Baldocchi and Meyers*, 1998], and in compliance with the guidelines of FluxNet, AmeriFlux and CarboEuro [*Kaiser*, 1998]. We recognize that eddy correlation measures of CO_2 flux density have become a standard protocol for estimating CO_2 exchange at the ecosystem level [*Grace*, 1995; *Aber et al.*, 1996; *Vourlitis and Oechel*, 1999]. The eddy covariance technique applied here is based on the assumption that the flux of a given scalar parameter can be measured as an average of the covariance between the 20-Hz fluctuations in the vertical wind speed and the 20-Hz fluctuations of the scalar parameters. This technique is valid for measuring surface fluxes if turbulent transport exceeds molecular diffusion, the flux of a given parameter is independent of measurement altitude, and there are no sources or sinks for the given parameter above the surface of the footprint being measured [*Gash*, 1986; *Kaimal and Gaynor*, 1991; *Kaimal and Finnigan*, 1994]. The maximum variation across the topographical relief (elevation) within the upwind fetch area was approximately 10-15 m, which minimizes the potentially important effects of hills and valleys on wind streamlining and, thus, surface fluxes [*Raupach et al.*, 1992]. Also, a high degree of homogeneity occurred for hundreds of meters in all directions from the measurement tower. The average height of the dominant sage species was near 25 cm, varying from about 10 to 70 cm for individual plants, and was the tallest species at the site [*Willson*, 1999; *Hill*, 2001]. Thus, no sources or sinks of mass or energy existed in the atmosphere above the top of the sagebrush canopy, although the sagebrush stand is considerably open with exposed soil surface cover ranging from about 30% in the spring to almost 50% by middle to late summer.

[13] The specific eddy covariance system used here is described by *Zeller et al.* [1989] and *Massman et al.* [1990] where concentrations of CO_2, air temperature, wind speed and direction are measured in three dimensions within a fast-response system. Flux density of CO_2, momentum, sensible and latent heat are then computed. Standard meteorological sensors are also permanently mounted for routine weather measurements [*Musselman*, 1994]. The eddy-covariance system was mounted at a height of 2.6 m on a Rohn 20G meteorological tower with an up-wind fetch of >500 m. The instrument platform included an ultrasonic orthogonal vector anemometer (model SATI-3VX, Applied Technologies, Inc., Longmont, Colorado), an infrared H_2O/CO_2 gas analyzer (model 6262, LiCor Inc., Lincoln, Nebraska), an ultraviolet krypton hygrometer, a cup anemometer, a wind vane, an air temperature and relative humidity sensor, a wetness sensor, a soil temperature sensor, a CR10 data logger (Campbell Scientific, Logan, Utah), an atmospheric microbarograph (Vaisala Inc., Woburn, Massachusetts), plus a net radiation sensor and a soil heat flux sensor (Radiation Energy Balance, Inc., Seattle, Washington). Measurements

were taken at a frequency of 20 Hz and consisted of the following parameters: orthogonal wind velocities, virtual air temperature, CO_2 and H_2O concentrations, and the temperature and pressure of the gas sample cell. The three-dimensional ultrasonic vector anemometer was mounted on the tower at a height of 2.6 m with a boom compass orientation of 295° (selected from predominant wind climatology). The sonic anemometer samples the wind at a 200 Hz rate and then constructs a 0.05-s (10-point) nonoverlapping block average to provide a 20-Hz data series. The cup anemometer and analog wind vane were mounted at a 3.0 m height downwind of the mean wind direction (270°). The sole purpose of the cup anemometer and wind vane was to verify proper operation of the ultrasonic anemometer.

[14] Analog signals input to the data packer from the scalar instruments were also sampled at 200 Hz and then processed by a 12-pole 100-Hz Sallen-Key low-pass filter before being block averaged. Digital and analog filtering and averaging minimized the effects of aliasing high-frequency spectral energy into the region below the 5-Hz Nyquist frequency [*Kaimal and Gaynor*, 1991]. The fast-response data acquisition system was composed of a laptop computer and data packer (Applied Technologies, Inc., Longmont, Colorado). Software for the data acquisition program (National Oceanic and Atmospherics Administration, Atmospheric Turbulence and Diffusion Laboratory, Oakridge, Tennessee) (T. Myers, personal communication, 1999) was modified to apply fifth- and third-order calibration polynomials for the LI-6262 CO_2 and H_2O signals, respectively. This software was also modified to provide the linear calibrations for the temperature and pressure signals. Three-dimensional, coordinate rotations were applied to variances and covariances resulting in zero mean vertical and transverse wind speeds, as described by *McMillen* [1988].

2.6. Community Chamber

[15] In the case of the community flux chamber (1 m^2), all measurement plots were chosen to be representative of the dominant sagebrush, grass, and forb community determined previously for the site and at numerous locations along the airplane transect (Table 1). Dark respiration was also measured for all plots by placing an opaque cover over the chamber and allowing 2–3 min for equilibration. Thus, the community chamber included both photosynthetic and respiratory components that included leaves, branches, and soil, while the branch cuvette included only leaves and branches of the dominant species (total cover >90%). Soil respiration was estimated from the difference in net flux between the branch cuvette and community chamber, plus the amount of plant surface area inside the chamber.

[16] Net CO_2 flux measurements were made using a closed-flow infrared gas analyzer (IRGA, LiCor 6200, Lincoln, Nebraska) [*Vourlitis et al.*, 1993] coupled to a clear Lexan chamber [*Vourlitis et al.*, 1993; *Jones et al.*, 1998; *LeCain et al.*, 2000; *Welker et al.*, 2000]. Twelve plots were selected based on a representative species composition (percent cover) and exposed ground surface (Table 1), as well as the apparent health of individual plants within the plot. Half of the measurement plots contained an individual sagebrush plant that dominated the total leaf area inside the chamber, while half of the total plots contained only grass and forbs. Mean CO_2 flux values were computed for the site based upon the vegetation data shown in Table 1; that is, flux values measured for quadrats with different percent cover of sage versus grass and forb species were weighted proportionally and then averaged based on the percent cover and leaf area per unit ground area values determined for the intensive site (not significantly different from other transects along flight line) and presented in Table 1.

[17] Net CO_2 exchange was measured by placing the 40-cm-high, 1-m × 1-m chamber over an undisturbed 1-m^2 plot. The chamber was sealed to the ground at the time of measurement using a shallow groove (<5 cm depth) in which the rim of the chamber was positioned to provide good soil contact along the entire perimeter of the chamber. The air inside the chamber was mixed with four small fans that generated wind flow of ~40–140 cm/s depending on locations inside the chamber. Three sequential measurements of net photosynthetic CO_2 exchange were taken for each plot. CO_2 exchange was measured for three consecutive 15- to 30-s periods immediately after the chamber was settled onto to the sample plot. Between measurement sets, the chamber was opened to the atmosphere until ambient CO_2 levels were approached to within ±10 μL/L. Environmental parameters such as air temperature, humidity and incident sunlight (PAR) were monitored simultaneously with CO_2 exchange measurements both inside and outside the chamber at the time of measurement. Similar estimates of respiratory CO_2 flux (soil and plant) were made using an opaque covering around the entire chamber. All measured parameters inside the chamber matched ambient values by at least ±16% for all comparisons of CO_2 flux values measured concomitantly with the aircraft, tower, and the branch cuvette systems.

2.7. Leaf/Branch Cuvette

[18] Photosynthetic performance on a leaf area basis for individual species was monitored for randomly selected plants during periods when the King Air was overhead and the tower and 1 m^2 chamber measurements were also underway. One to three shoots on each of 10 plants were sampled alternately during the entire period of aircraft sampling (~1–2 hours) in both the dominant shrub and grass/forb species. For the dominant sagebrush, three replicate measurements of all 10 plants were usually possible during the total time (~2 hours) the aircraft was overhead. Additional measurements were made for up to 2 hours before and after the aircraft sampling periods and on the day before or after flight days. Individual sample branches were selected based on appearance (healthy appearing foliage) and leaf age class (~1–3 years old). Foliated branch segments (~8–10 cm) were enclosed in gas-exchange cuvettes of a LICOR 6200 portable photosynthesis system. Mean flux values reported here were computed for the 15-min measurement intervals when the aircraft was overhead and measuring CO_2 fluxes along the flight transect. Additional gas exchange measurements were made on adjacent grass and forb species.

[19] Photosynthetic CO_2 flux was computed on a total leaf area basis as described in detail by *Smith et al.* [1991]. These values were then converted to a unit ground area basis from measurements of total leaf area (one-sided) per unit ground area for each of the dominant species (sage-

brush, grasses, and forbs) that were present at the time of measurement (Table 1). Leaf and air temperatures, air humidity, and photosynthetic photon flux density (PPFD) were also measured simultaneously with photosynthetic gas exchange measurements inside the cuvette, as well as the same values for ambient conditions outside the cuvette at the time of measurement. In general, the measured parameters inside the cuvette (air temperature, relative humidity, and leaf temperature) matched those of the ambient surroundings by at least ±19% during measurement intervals.

2.8. Standardization and Area Conversions

[20] Because the height of both the aircraft and tower measurement systems were well above the maximum height of the plant canopy of this landscape, tower and aircraft measurements were assumed to be comparable in terms of CO_2 flux estimates. The 1-m^2 chamber measurements also incorporated both plant and soil measurements of CO_2 exchange, although these individual 1-m^2 plots could vary according to plant species composition and exposed ground cover in comparison to mean values by the tower or aircraft. Also, fan-generated air circulation patterns inside the chamber could alter boundary layer effects inside the chamber versus outside, especially during morning hours (time of aircraft sampling) when wind speeds tended to be low at the site. Finally, the branch cuvette measurements for sagebrush plants included mostly leaves, but also a small amount of woody branch material. Thus, to compare absolute values of CO_2 flux density generated from cuvette and chamber measurements with tower and aircraft values, all values of CO_2 flux were converted to μmol CO_2 m^{-2} s^{-1}, expressed on a unit ground area basis. Branch cuvette values for measured CO_2 flux for the sagebrush, grass, and forb species were weighted proportionally according to corresponding measurements of total leaf area (one leaf side) per unit ground area at the site (Table 1), as well as along the aircraft flight transect. Specifically, mean flux measurements for each type of plant were converted to a unit ground area flux by weighting flux values for each plant type (sagebrush, grass, forb) according to the mean proportions of leaf area per unit ground area determined from all transect samples along the flight line. Because leaves were measured predominantly by the branch cuvette, with very little stem area involved, a more accurate respiratory term (plant and soil) was measured by the darkened 1-m^2 chamber, or by subtracting leaf/branch fluxes from chamber fluxes to obtain soil flux. This value for soil flux could then be added to the leaf cuvette flux values (with appropriate weighting for the large leaf/soil area ratio). Thus, all branch cuvette measurements of net CO_2 exchange of leaves (and small stem amounts) were corrected for respiration by using the 1-m^2 chamber values of plant/soil respiration (same-day measurements) in natural light and experimental dark conditions. Overall, soil CO_2 flux was never >19% of leaf flux values for the sample dates described here.

3. Results and Discussion

[21] The magnitudes of both temporal and spatial errors in measuring CO_2 flux density were evaluated by comparing same-day measurements with measurements taken on different days using all four measurement systems (cuvette, chamber, tower, aircraft). To minimize temporal variability, Table 2 shows both absolute values and relative comparisons of CO_2 flux density when same-day measurements were taken simultaneously within an approximate 2-hour morning period (∼0900–1100) using all four instrument systems on the June and July sample days. Absolute CO_2 flux densities were within the ranges reported for a variety of ecosystem types [see *Kelly et al.*, 2002, Table 4; *Baldocchi et al.*, 2001a]. The June sampling dates (June 21 and 22) generated some of the greatest net CO_2 flux values measured for the summer of 2000, while the July 7 sample date generated the lowest values measured during midsummer due to a prolonged period without significant precipitation prior to this date. From June 14 to June 21, only 25.8 mm of precipitation had accumulated (five rain events of >2 mm., followed by an additional accumulation of only 4.8 mm by the next sampling date (July 7). As a result, minimum predawn plant water potentials decreased from greater than −1.0 MPa measured on June 21 to less than −2.5 MPa on July 7 (J. R. Hill and W. K. Smith, manuscript submitted to *Ecology*, 2002). Correspondingly, all four measurement systems recorded fluxes of CO_2 that were almost twice as great during June than for July 7 (Table 2). In addition, mean daytime CO_2 flux values were positive (net uptake of CO_2) and statistically similar (ANOVA, p = 0.05) between all four measurement systems after proportional corrections for differences in plant leaf area per unit ground area, species composition, and exposed soil surfaces (e.g., soil respiration). Moreover, relative declines in CO_2 flux values measured between the two sampling dates (high and low plant water status) were also statistically similar (ANOVA, p = 0.05) for the aircraft (−53%), tower (−50%), chamber (−39%), and the leaf/branch cuvette system (−54%) (Table 2). Differences in measured CO_2 flux among the four instrument systems were also not statistically significant at p = 0.05 using a two-sample *t* test, despite high variances (>100% of some mean values) during the two periods of either high or low flux values [*Zar*, 1999].

Table 2. Concurrent (0900–1100 Hours True Solar Time) Measurements of Net CO_2 Flux Density (μmol CO_2 m^{-2} s^{-1}) Using the Four Different Instrument Systems on Days With Relatively Low (<2.5 MPa) and High (>1.2 MPa) Water Potentials at the Peak of the Summer Growth Season, 2000[a]

Instrument System	June 21/22	July 7	Percent Difference
Aircraft	4.2 ± 0.6	2.2 ± 0.3	−53
Tower	4.0 ± 0.7	2.0 ± 0.4	−50
M^2 chamber	4.1 ± 1.6	2.5 ± 0.8	−39
Branch cuvette	4.6 ± 1.1	2.1 ± 0.5	−54
Mean difference ±range, %	6 ± 10	9 ± 14	6 ± 14

[a]The aircraft and tower systems employed the eddy covariance technique, while the 1-m^2 chamber and leaf/branch cuvette utilized standard CO_2 gas exchange methods (see text). All values are expressed on a per unit ground area basis (see text for further details) and ±values are 95% confidence intervals. No statistical differences in flux values were found for comparisons of individual means with group means among all four measurement systems on either date (ANOVA, N = 12–38, p = 0.05). Mean percent difference is computed as the percent difference between each system and the aircraft flux value, while range is the largest difference also expressed as a percent.

[22] To evaluate temporal errors in CO_2 exchange measurements among the four different measurement techniques,

Table 3. Net CO_2 Flux Density (μmol CO_2 m^{-2} s^{-1}) Measured for Sagebrush Steppe Using the Four Different Instrument Systems (Leaf/Branch Cuvette, 1-m^2 Chamber, and Tower)[a]

	1 Day		2 Days		4 Days		1 Week		2 Weeks		
Instrument System	Flux Density	N	Flux Density	N	Flux Density	N	Flux Density	N	Flux Density	N	Mean Difference ± Range, %
Aircraft	4.4	–	4.4	–	4.4	–	4.4	–	4.4	–	–
Tower	4.5	4	4.7	6	4.9	12	3.7	21	2.9	42	14 ± 34
1-m^2 chamber	3.9	13	3.6	17	3.7	19	2.9	21	2.7	34	24 ± 38
Cuvette	4.7	13	4.9	20	4.8	26	3.3	32	3.6	47	14 ± 29
Mean difference ±range, %	7 ± 11		12 ± 18		14 ± 18		25 ± 34		31 ± 38		18 ± 24/14 ± 33

[a]Measurements were not taken on the same day, but at the same time of day (0900–1100 true solar time) and within the indicated number of days (N) before or after the closest day of flight measurements (May 15 to August 1, 1999–2000). The total number of aircraft flights was 13, with 10 occurring between May 30 and September 10, 1999, and one each on June 21, 22, and July 7, 2000 (Table 2). All values are means for the total number of days (N) that measurements were taken before or after individual flight days. Column means and range represent measurement errors due to instrument type, while row means estimate errors due to temporal separation between measurements taken with the same instrument system. All mean difference values are expressed relative to the aircraft value of 4.4 mol m^{-2} s^{-1}.

measured values from each of the three instrument systems were compared to aircraft measurements taken on different days, but at the same time of day (Table 3). From data generated on a total of 13 flights in 1999 and 2000, the differences in measured CO_2 flux between each instrument type and the aircraft increased curvilinearly ($f(x) = -1.28x^2 + 3.77x + 3.51$, $R^2 = 0.91$ [*Zar*, 1999]) according to the number of days separating measurements (Table 3). When measurements were separated by less than 3 days, differences between the mean flux values for the three ground-based instrument systems and aircraft values had a maximum variation of ±12% with a range of from 11% to 18%. When measurements were separated by 1- or 2-week spans, this difference increased to ±25% and ±31%, respectively, and 34% and 38%, respectively. Thus, day-to-day variability in flux values for a given instrument platform was greater than between-instrument variability only when the time before or after aircraft measurements was greater than about 4 days (Table 3).

[23] A similar study compared CO_2 fluxes measured for an artic tundra landscape using both a CO_2 gas exchange chamber (0.5 m^2) and an eddy covariance tower and aircraft system [*Oechel et al.*, 1998], although leaf/branch level measurements were not reported. Also, the flight transect was located some distance away from the intensive measurement sites (up to ~30 km for one intensive site) and only tower and chamber measurements were compared for the same day. Even so, aircraft net flux values during the day were comparable when greater turbulent mixing occurred, although relatively large differences between chamber and tower flux measurements occurred at night when boundary layer conditions were much more stable [*Oechel et al.*, 1998]. During daylight hours, chamber and aircraft flux values were generally lower than tower measurements (~23 to 28%), and was assumed to be due to spatial and temporal sources of variation. However, these comparisons of net ecosystem flux were surprisingly similar in magnitude considering the spatial and temporal variability that occurred between the three different instrument systems. A similar error in the branch cuvette (fan air mixing) may not be as significant due to the absence of a soil surface respiration component and the relatively low surface area and respiration from stem material relative to leaf values.

[24] Net CO_2 flux density measured using the 1-m^2 community chamber were consistently lower in value compared to the other measurement systems for all comparisons made for days before and after aircraft flights (Tables 2 and 3). This is consistent with the findings reported by *Oechel et al.* [1998] where chamber values for CO_2 flux were lower than tower values, especially at night. They hypothesized that the lower chamber fluxes could be due to especially poor turbulent mixing (ambient) at night, as well as chamber heating during the day (although chamber/tower differences were not apparent in the data presented). Chamber heating during daytime measurements was thought to potentially increase respiration over photosynthesis and, thus, decrease net flux values. Because of the care taken in the current study not to include measurements for when the chamber was over 2°C above ambient air temperature (favoring a higher respiration component), it is possible that the increased turbulence generated by the chamber fans could have created more greater transfer from the soil surface (respiratory CO_2 source), decreasing measured net flux values. A check of wind speeds inside the chamber using a hot-wire anemometer (Hastings, model 1100A) revealed that chamber airflow was significantly greater near the soil surface than outside the chamber. For example, wind speed at the soil surface (within 0.5 cm height above soil surface) was almost threefold greater than ambient wind speeds of approximately 0.2–0.4 m s^{-1}. Ambient wind speeds were generally light (<0.60 m s^{-1} during the morning hours at 2 m above the ground surface), increasing the possibility of a stabilized boundary air layer next to the soil surface that could have been disrupted by the fans inside the gas-exchange chamber.

[25] NET CO_2 flux values measured from the aircraft and tower eddy covariance systems were considered comparable in terms of methodology and instrumentation. Both systems measured net CO_2 exchange that included photosynthetic (leaves) and respiratory components (branches and soil surface), although with substantially different footprints sizes. Also, significant differences in boundary air layer effects on CO_2 exchange are still a possible source of error [*Massman and Lee*, 2002]. For example, the tower could be situated above a relatively thick, still-air boundary layer during the early morning hours when winds are calm, enabling radiational cooling, plus cold-air drainage and settling, to generate a stable inversion in air temperature. Mass fluxes at tower height coming from this more stagnant boundary air layer could be slower than outside the boun-

dary layer where turbulent flow could enhance eddy transport an order of magnitude, or more [*Massman and Lee*, 2002]. Variability in CO_2 flux may also be attributed to short-term changes in site conditions (e.g., soil moisture, air temperature, and soil temperature), even though all measurements were taken over the same 2-hour interval during midmorning. In addition, some of the scatter undoubtedly stems from uncertainties inherent in the eddy-correlation flux technique [*Lenschow and Stankov*, 1986].

4. Summary and Conclusions

[26] Scaling upward from the leaf/branch cuvette to an aircraft system for measuring CO_2 flux increases the footprint size of the measurement, decreases mechanistic resolution at the species level, and also requires a substantial increase in initial equipment costs. The relatively close correspondence in values reported here between the four instrument systems indicates that each of the four instrument systems may represent viable alternatives for estimating CO_2 source/sink activities in certain terrestrial ecosystems. However, the degree of homogeneity in topography and vegetation structure, along with the open nature of the plant canopy, may represent a rather ideal situation whereby leaf-level fluxes are also indicative of canopy fluxes. For this type of ''least-error'' ecosystem, adequate spatial sampling using a leaf/branch cuvette could provide accurate estimates of ecosystem flux, especially if used in combination with a chamber designed for measuring soil respiration independently. Because plant-level measurements provide a more mechanistic approach, along with a high potential for controlled experimentation, leaf/branch approach in similar ecosystems would also enable an evaluation of species-specific responses to environmental factors influencing CO_2 exchange (e.g., global change parameters). Ultimately, these data would also provide the basis for future modeling efforts to predict the impacts of such activities as land-use management or changes in biodiversity. However, additional comparisons are needed for other landscape types, especially those with greater structural complexity, before the accuracy of one measurement approach versus another can be evaluated more comprehensively. It might be expected that increased structural and aerodynamic complexity (e.g., forests) might involve, for example, a greater internal recycling of plant and soil CO_2 and more variable photosynthesis at the branch level. This added complexity might also generate an insurmountable sampling problem at the level of a gas exchange chamber.

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